**Title:** *Landscape Context mediates the effect of shortening fire intervals in boreal systems*

**Abstract:**

Warming temperatures have been linked to increased frequency and severity of wildfires across a variety of ecosystems. This trend is especially apparent in the boreal, where time intervals between fires have been decreasing from 50-100 years to 10-15 years within the last three decades. Shortening fire intervals have been shown to drive changes in successional pathways in semi-serotinous boreal forests via seedbank limitation, but the role of landscape context in promoting resiliency to increasing disturbance remains unclear. To investigate how landscape context alters the resilience of species to shortening fire intervals, we established plots across a gradient of fire histories (1-3 fires in 70 years) in two sites of Interior Alaska. We compared recruitment between conifers, deciduous trees, shrubs and graminoids and sampled across factors such as differing hydrology, slope, aspect and elevation. All stands were originally dominated by black spruce (*Picea mariana*), but black spruce recruitment was significantly lower following three fires, compared to unburned stands and stands burned once under longer fire return intervals. Recruitment of shrubs and graminoids increased after two fires, and was further solidified after three fires, indicating a transition to shrubland and grassland ecosystems occurring via shortening fire intervals. Measurements of organic soil layers show that organic layers in dry, sloped sites – but not flatter, higher moisture sites – became more homogenous after multiple fires, indicating the importance of landscape context. Our results show that local variations in hydrology and slope may mediate the effects of shortening fire intervals by introducing heterogeneity in organic soil consumption and seedbank availability. Results of this study offer strong empirical evidence that landscape context may promote resiliency to changes in local disturbance regimes.

**Introduction**

Increasing temperatures have been linked with global increases in the frequency and intensity of wildfires, sparking concern that changing fire regimes will lead to rapid ecosystem change if local resilience is exceeded (Young et al. 2017). Warming in high latitude environments is taking place faster than any other environment and due to this, local fire regimes may have already surpassed historical ranges of variability: Fire return intervals in the boreal forests of Interior Alaska have shrunk from an average of 100-300 years to 10-20 years in the last six decades (Kasischke et al. 2010, Brown & Johnstone et al. 2012, Johnstone & Chapin 2006A, Johnstone & Chapin 2006B). Shortening fire intervals have been shown to alter successional pathways through seedbank and substrate consumption, and theoretical model outputs suggest that an increase in area reburned in short intervals may lead to a shift in forest community composition from conifer-dominated stands to deciduous shrublands and grasslands (Johnstone et al. 2009, Hoy et al. 2016). Initial empirical observations of two fires in short periods in boreal system indicate increases in the presence of deciduous species after fire, but the specific effects of three or more fires each occurring within a few decades remains unknown, limiting our ability to make inferences regarding future boreal forest community composition. Studying postfire regeneration in the boreal system is essential to understanding and predicting the impact of ongoing environmental and climatic change in high-latitude environments.

We hypothesize that the specific mechanism responsible for the reduction in conifer reestablishment after multiple fires is the depth of organic layer. Organic layers tend to be relatively thick in boreal forests and are often capped with a thick layer of moss or sphagnum. The presence of this layer favors conifers: Conifers (including black spruce) rely on large aerial seedbanks produced from semi-serotinous⁠ cones after a fire to reproduce. The quantity of seed produced means that conifers are able to establish on thick organic layer, whereas deciduous species often only recruit from seed on exposed mineral soil. High-severity fires may consume organic layers, therefore enabling deciduous species the reproductive advantage over conifers. Repeated fires in particular may prevent the reestablishment of organic layers entirely (Johnstone et al. 2009, Brown and Johnstone 2012, Brown et al. 2015).

This study set out to characterize post-fire regeneration after three short-interval fires in a black spruce forest in Interior Alaska. We hypothesis that a reduction in organic soil layers disadvantages conifer regeneration, promoting a transition of black spruce stands into shrublands and grasslands dominated by deciduous species. We anticipate that dry, sloped sites may be less resistant to this transition due to the more homogenous effect of frequent fire on local organic soil layers. The effects of multiple, short-interval fires on boreal successional trajectories may be mediated through organic soil consumption and loss of seedbank. We tested these hypotheses by documenting patterns of succession and site conditions in stands of varying fire history.

**Methods**

**Site Selection**

We established 46 different 20m-by-20m plots in two sites in Interior Alaska in natural mosaics of stands differing in recent fire history. Each plot has experienced between one to three fires with full aboveground canopy mortality in the last 60 years, as confirmed by aerial photography (Supplement 1). Several unburned plots were established as controls. Plots were established a minimum of 50 meters apart, and at a reasonable distance from seed source outliers.

Plots were stratified between an upland site and a lowland site. The upland site was selected as a representative of Interior forests more generally. The lowland site was established at a site east of Fairbanks in a region that has a slightly wetter substrate and a slightly more heterogeneous topography. Examining both allows us to investigate the effect of local hydrology in mediating the impacts of multiple fires.

Locations were selected by….

Size of plots, slope and aspect taken from XXX source…

Presence of spruce prior to the burn sequence was verified via…

Need something here about dates of fires, locations, mean annual temps, mean annual precip. Suggest a table…

Two processes facilitate the formation and assembly of a plant community within a given environment: colonization and establishment. Colonization refers to the arrival of a seed or seeding at a location while establishment describes the ability of an individual to survive and grow in that particular environment. Distinguishing between the two is important: different factors govern each of the two processes (Johnstone et al. 2009, Brown et al. 2015).

Regeneration was measured using two metrics used to distinguish between colonization and establishment in the field: incoming recruitment and established recruitment. We define incoming recruitment here as seedlings under diameter breast height (DBH, or 1.3 meters). Established recruitment, therefore, refers to plant individuals that have grown above DBH. Individuals of each category were counted according to species type within subsets of each plot. Plot stem count data was pooled within a site to obtain standardized measurements, then scaled to stem count per hectare and log-transformed unless otherwise noted. Graminoid presence was estimated as percent cover in 1-meter subsets of plots.

Soil samples were taken at 5 points at each site (at each corner and in the center) with a XX inch AMS soil core sampler to a depth of…. Soil type percent cover was estimated across 1-meter subplots at each corner of each site.

**Data Analysis**

**[Spatial autocorrelation paragraph]**

To test the association between substrate consumption and regeneration, a linear mixed effects model was used to examine the connection between species regeneration and organic layer depth controlling for number of fires and site type as a random effect.

**Results**

**Site Description**

Sites were established across a range of slopes and aspects (Fig. X). [This is actually a question I had – our sites aren’t really evenly established across slope. Aspect’s a little more even, but most of our sites tend to have more gentle slopes. This isn’t really a steeply sloped area, so can we make the argument that they’re essentially representative? Histograms in the comments for reference – thinking about putting them in the supplement ultimately]

**[Reconstruction of fires paragraph]**

**Conifer Regeneration**

Presence of colonizing conifers increases after one fire, indicating a pulse of advantageous regeneration following post-fire resource availability. The difference between conifer colonization and conifer establishment indicates the value in distinguishing between stages of recruitment. Both colonization and recruitment of conifers decline with increasing fires, though the decline in colonization occurs more quickly in upland plots (Fig. X).

**Deciduous regeneration**

Deciduous regeneration is generally higher in sites that have experience more fire, consistent with prior study. Presence of birch gradually increases with number of fires, particularly in lowland sites (Fig X). Birch abundance is more homogenous than salix abundance: both salix colonization and establishment abundance is much more variable between sites. Salix establishment declines after one fire but increases after three fires (Fig. X). Alder regeneration is generally lower and doesn’t exhibit a strong trend (Fig. X). Aspen colonization is high in lowland sites, and aspen establishment generally increases with fire (Fig. X).

**Graminoid**

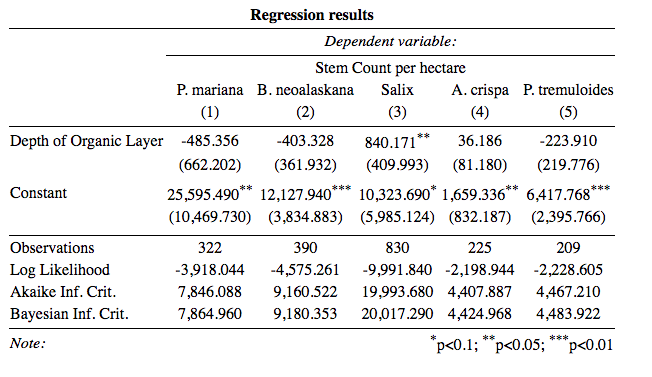
Heterogeneity in relative grass cover increases with number of fires, particularly in lowland plots. Average graminoid cover reaches a maximum in twice-burned lowland sites (23.6%) and twice-burned upland sites (41%) and declines to 4% and 26% respectively (Fig. X).

**Organic layer depth**

Unburned sites had an average organic layer depth of 18 cm, with outliers at 27 and 11 cm. (Fig X.) Organic layer depth diverged between the upland and lowland site: the average depth at once-burned upland sites was 6 cm, while the average organic layer depth at once-burned lowland sites was 10 cm. Average organic layer depths become more similar in three-burned plots between the two sites.

Percent cover of exposed mineral soil generally increased with number of fires, with the greatest amount of exposed soil found in lowland plots after three fires. Lowland plots had significantly more heterogeneity in the percent cover of exposed mineral soil compared to upland plots (Fig. X).

**Model Results**



Results from the linear mixed model indicate an association between organic layer depth and black spruce regeneration after controlling for the variation found between number of fires and site (p value = < 2e-16).

**Discussion**

**Regeneration**

Deciduous colonization does not decline across burn histories, indicating that deciduous colonization is not limited by multiple fires.

**Organic layers**

The divergent trend in organic layer consumption indicates the difference in fire effects between the upland and lowland sites: less organic layer is consumed in lowland sites with one or two fires, indicating that wetter conditions may mediate the effect of even high-severity fires. This variation between sites indicates that local heterogeneity in topography and climate may facilitate resilience in black spruce stands, up until a certain threshold.

**Conclusions**

The results of this initial work suggest that regeneration forests in Interior Alaska is in fact different after multiple fires. Conifer regeneration appears to be declining after multiple fires, likely because of smaller organic layers. This trend is unprecedented in our lifetimes: Black spruce forests are the dominant forest type in Interior Alaska and have been stable in the region for nearly six thousand years.

A threshold change in the stability of black spruce forests would have global implications: boreal forests are a global carbon sink, storing up to 50% of the world’s carbon currently stored in forests. Out of that 50%, the majority is locked up in frozen soils and permafrost beneath black spruce forests, and a shift to deciduous trees and shrubs may allow that carbon to be released, accelerating ongoing change. It is therefore essential to focus on documenting and understanding ongoing and future changes in the boreal forest region.